

TAXONOMY OF *PERITYLE*
SECTION *PAPPOTHRIX*
(COMPOSITAE — *PERITYLANAE*)¹

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This small section of the genus *Perityle* is comprised of five species which are distributed throughout Trans-Pecos Texas and in the Organ Mountains of southern New Mexico. Asa Gray (1852) proposed the section to include a species of *Laphamia* (now synonymous with *Perityle*), *L. rupestris*, which exhibited a unique pappus of about 20 bristles.

Rydberg (1914) elevated Gray's section to generic rank, apparently relying on the multi-bristled pappus as the primary distinguishing feature. Other species of *Perityle* have a pappus of 0-2(3) bristles (often 4-6 in *P. staurophylla*) with or without squamellae. Everly (1947), in her revision of *Perityle*, retained *Pappothrix* as a separate genus because the group "can be clearly defined on the basis of a pappus of 15-30 awns." *Pappothrix* indeed is characterized by its pappus, but as Macbride (1918), Shinnars (1959), and others have concluded, the distinction does not warrant generic status apart from *Perityle* where pappus variability is a hallmark. Considering most other morphological features *Pappothrix* and *Perityle* are quite similar, and this is substantiated by chromatographic evidence (Powell, 1968a). Sectional status is maintained for *Pappothrix* because the species comprise a natural phyletic unit within *Perityle*. Other information concerning the revised taxonomy of *Perityle* is presented elsewhere (Powell, 1968a).

ECOLOGICAL CONSIDERATIONS

Species of section *Pappothrix*, and in fact most all taxa of the genus *Perityle*, exist in rather bizarre habitats, occurring only in soil-filled crevices of otherwise solid rock.

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I am grateful to the curators of the various herbaria who loaned specimens utilized in this work. I also acknowledge Professor B. L. Turner who suggested the study of *Perityle* and contributed valuable counsel during the course of this investigation.

Plants may be distributed in perpendicular bluffs, large boulders, or any rock mass of considerable size and stability. Plants are never found growing in soil, even among smaller rocks at the base of cliffs. This would appear to represent very stringent conditions for the survival of these plants, especially in the arid southwestern United States. Examination of most populations reveals that a majority of the plants are relatively old, having developed strong, thick woody rootstocks. Dispersal of seeds seems to be effected by fortuitous deposition of achenes by wind and washing from summer thundershowers. No dispersal vectors such as birds or ants have been observed carrying achenes, but it is likely that such animals do spread seeds accidentally.

Plant genera with which the species of *Pappothrix* are commonly associated in their rock habitats are *Heterotheca* spp. and *Hedyotis* spp. Less often associated are *Selaginella* spp., *Galium* spp., *Crotalus lepidus*, and *Cirsium turneri*.

Greenhouse tests of all the section *Pappothrix* species have revealed that they are almost completely self-incompatible. This has facilitated hybridization experiments to the point of determining percent of seed-set, but achene germination is very poor. Manipulation of conditions has shown that dormancy at normal refrigerator temperatures increases the percent of germination about 30%. At present it is difficult to determine if poor germination is due to natural or induced phenomena.

The absence of self-compatibility brings out an unresolved question about pollen transfer under natural conditions. Plants in their natural habitat normally produce heads with a very high percent of well-developed achenes. Ants and various other small insects (such as beetles) have been observed visiting flowers and crawling over plants, but there is no evidence that these animals effect pollination.

There is no apparent regularity with which populations of section *Pappothrix* species are distributed in the hundreds of likely habitats available throughout the total distribution area. The most successful populations are usually located on north and east-facing bluffs or in narrow canyons

where the plants receive only partial sun, but in some areas which appear to offer ideal habitats, plants of these species have not been found. The surface geology of the Trans-Pecos region of Texas and adjacent areas provides important considerations for understanding the distribution of section *Pappothrix* species (Sellards, Adkins, and Plummer, 1958). In general, this region has been subjected to violent geologic events, including intrusive and extrusive Tertiary volcanic activity, cataclismic mountain-forming, faulting, and extensive erosion. Any wide-spread ancestral species of section *Pappothrix* (possibly *P. cernua*) would have become increasingly more isolated with progressive erosion especially because of the restricted habitats. Occupation of new habitats by expanding populations appears to be controlled by fortuitous dispersal, regardless of the desirability of a location. There is some indication that a positive correlation exists between geological events and biological evolution in *Perityle*, but it is not advisable to speculate extensively at this time.

CHROMOSOMAL STUDIES

Meiotic chromosome numbers have been compiled with the utilization of methods similar to those outlined by Turner and Johnston (1961). Voucher specimens are deposited in the Sul Ross State College Herbarium.

Chromosomes of all section *Pappothrix* species are heteromorphic in size, with 2-3 bivalents being smaller and 2-3 bivalents being larger than the others. One or 2 of the smaller bivalents often divide precociously at anaphase I, and thus could lead an observer to believe that unpaired univalents, fragments, or extra chromosomes are occurring. However, careful observation has demonstrated that meiosis is regular in diploid ($n = 17$) and polyploid ($n = 34, 68, 85$) plants.

The chromosome numbers presented in Table I are the first reports for each species of section *Pappothrix*. All species so far examined exhibit diploid chromosome numbers with the exception of *Perityle cinerea*. Diploid and polyploid numbers have been recorded for *P. rupestris*.

Chromosome numbers have not been particularly helpful in determining the interspecific taxonomic relationships within section *Pappothrix* or the affinity of it with sects. *Laphamia* and *Perityle*. The basic number of *Pappothrix* seems clearly established as $x = 17$. Aneuploid numbers above and below $n = 17$ exist in several species of *Perityle* (Powell, 1968b), and it is possible that the ancestral basic number for the genus *Perityle* is $n = 18$ or 19 , but the preponderance of species exhibit chromosome numbers of $n = 17$ or polyploids thereof.

Populations of *P. rupestris* seem to possess a remarkable ability to establish polyploidy. Populations with diploid, tetraploid ($n = 34$), octaploid ($n = 68$), and decaploid ($n = 85$) chromosome numbers have been discovered (Table I). The explanation for this high polyploid tolerance is not clear at this time. Perhaps a partial solution is correlated with the stringent ecological conditions under which the species live, and their perennial habit. Also, H.

Table I. Species of *Perityle* section *Pappothrix* Examined for Chromosome Number.

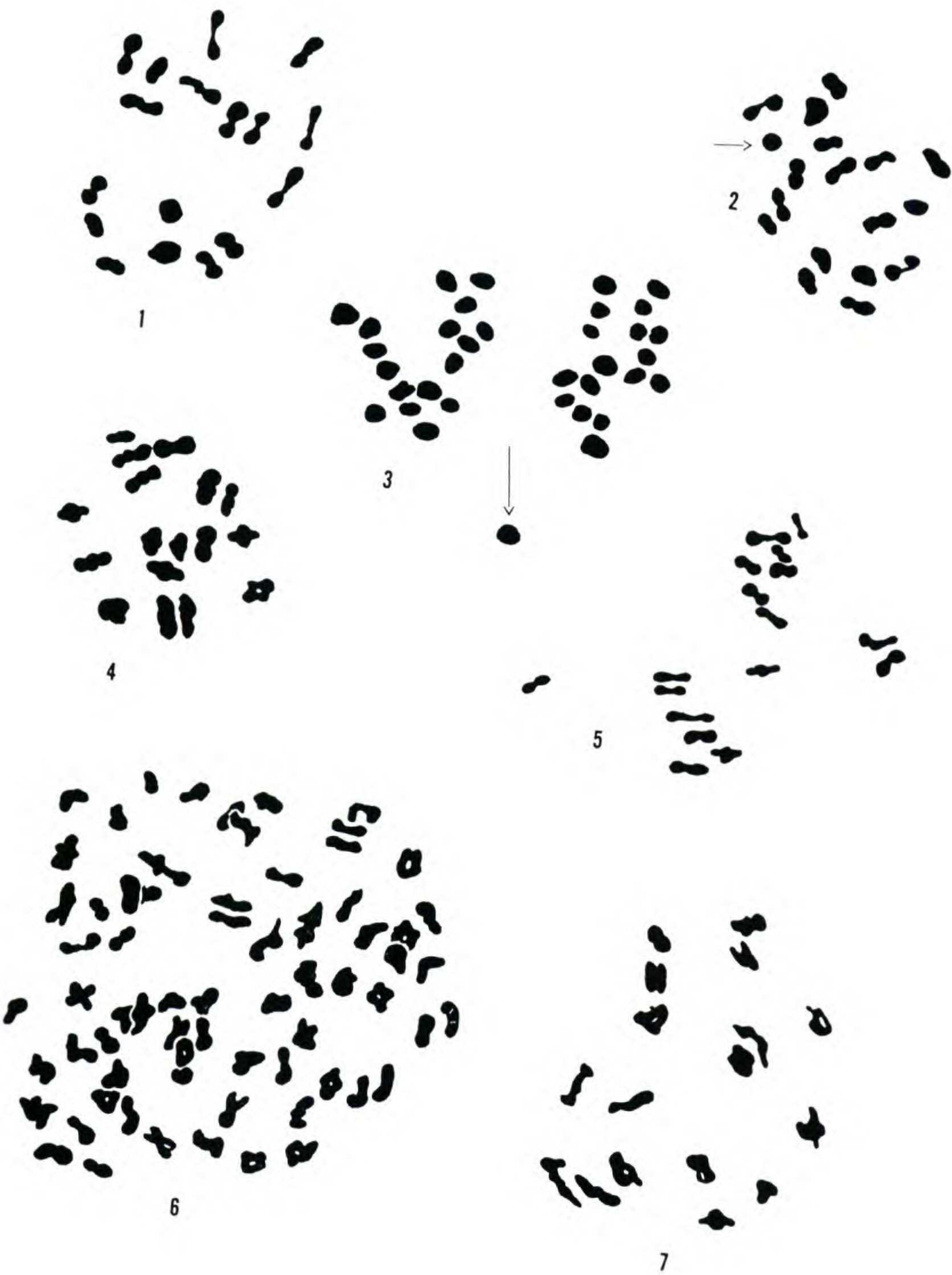
Species	<i>n</i> Number	Location and Voucher
<i>Perityle cernua</i>	17 + 1 frag.*	NEW MEXICO: Doña Ana Co. Dripping Springs Canyon. <i>Sikes & Babcock 328</i> .
<i>P. cinerea</i>	ca. 68	TEXAS: Pecos Co. 6 mi. e. of Bakersfield. <i>McKenzie 128</i> .
	ca. 68	TEXAS: Pecos Co. 7-Mile Mesa, near Ft. Stockton. <i>Powell 1274</i> .
<i>P. vitreomontana</i>	17	TEXAS: Brewster Co. n. side, Glass Mts. <i>Warnock & Powell 19111</i> .
	17*	TEXAS: Brewster Co. n. side, Glass Mts. <i>Sikes 110</i> .
<i>P. quinqueflora</i>	17	TEXAS: Culberson Co. s. McKittrick Canyon, Guad. Mts. <i>Powell 1246</i> .
	17	NEW MEXICO: Eddy Co. 6 mi. w. of Whites City. <i>Powell 1319</i> .

Species	<i>n</i> Number 17*	Location and Voucher
		TEXAS: Jeff Davis Co. ca. 20 mi. w. of FM 2017, San Carlos Tunnel. <i>Sikes & Babcock 326.</i>
<i>P. rupestris</i> var. <i>rupestris</i>	17	TEXAS: Jeff Davis Co. 17 mi. n. of Alpine. <i>Powell 1229.</i>
	17	TEXAS: Jeff Davis Co. Boy Scout Camp, n. of Ft. Davis. <i>Sikes 33.</i>
<i>P. rupestris</i> var. <i>rupestris</i>	17	TEXAS: Jeff Davis Co. 10 mi. n. of Alpine, near Mitre Peak. <i>Sikes 4a.</i>
	ca. 17	TEXAS: Jeff Davis Co. Madera Canyon, n.w. of Ft. Davis. <i>Sikes 18.</i>
	34	TEXAS: Jeff Davis Co. Madera Canyon, n.w. of Ft. Davis. <i>Sikes 17.</i>
	34	TEXAS: Jeff Davis Co. Madera Canyon, n.w. of Ft. Davis. <i>Sikes 19.</i>
	ca. 34	TEXAS: Jeff Davis Co. 2 mi. n. of Ft. Davis. <i>Powell 1228.</i>
	34	TEXAS: Jeff Davis Co. Davis Mt. State Park. <i>Sikes 15.</i>
	ca. 34	TEXAS: Jeff Davis Co. 6 mi. n.w. of Ft. Davis. <i>Sikes 16.</i>
	34	TEXAS: Jeff Davis Co. 6 mi. n.w. of Ft. Davis. <i>Sikes 15.</i>
	ca. 34	TEXAS: Jeff Davis Co. Timber Mt., n. of Ft. Davis. <i>Sikes 45.</i>
	34	TEXAS: Jeff Davis Co. 16 mi. n. of Alpine. <i>Powell 1316.</i>
	34 II + 1 frag.	TEXAS: Jeff Davis Co. 11 mi. n. of Marfa. <i>Powell 1550.</i>
	68*	TEXAS: Jeff Davis Co. 13 mi. s. of Toyahvale. <i>Sikes 91.</i>

Species	<i>n</i> Number	Location and Voucher
<i>P. rupestris</i> var.	17	TEXAS: Brewster Co. 6 mi. n. of Alpine. <i>Sikes</i> 2.
<i>albiflora</i>	ca. 17	TEXAS: Brewster Co. Basin, Chisos Mts. <i>Sikes</i> 31.
	17	TEXAS: Brewster Co. n. side, Cathedral Mt. <i>Sikes</i> 29.
	17	TEXAS: Presidio Co. s. side, Goat Mt. <i>Sikes</i> 48.
	17	TEXAS: Jeff Davis Co. 10 mi. n. of Alpine, near Mitre Peak. <i>Sikes</i> 4b.
	17	TEXAS: Brewster Co. 12 mi. s. of Marathon. <i>Sikes</i> 20, 21, 22.
	17*	TEXAS: Brewster Co. 17 mi. s. of Marathon. <i>Powell</i> 1408.
	17	TEXAS: Brewster Co. 3 mi. W. of Alpine. <i>Powell</i> 1320.
	ca. 34	TEXAS: Presidio Co. 9 mi. s. of Marfa. <i>Powell</i> 1237.
	ca. 34	TEXAS: Presidio Co. 10 mi. s. of Marfa. <i>Powell</i> 1238.
	34	TEXAS: Presidio Co. n.w. side, Goat Mt. <i>Sikes</i> 30.
	ca. 34	TEXAS: Brewster Co. Sunny Glen, 4 mi. w. of Alpine. <i>Sikes</i> 1.
	ca. 85	TEXAS: Brewster Co. 12 mi. s.e. of Alpine, Doubtful Canyon. <i>Sikes</i> 93.

*Indicates chromosome drawing.

Lewis (1967) has suggested "that autopolyploids may have a tremendous advantage over diploids at the time of the establishment of new colonies from a single normally outcrossing individual." The mechanism for the origin of polyploid populations is not apparent. The close morphic similarity of polyploids and diploids suggests autopolyploidy as the most logical mechanism, although, as mentioned above, meiosis even in high polyploids appears regular with no



multivalent configurations observed. However, if all polyploid populations which have been examined are old and well established, it is likely that any meiotic irregularities would have been eliminated. W. Lewis (1967) and H. Lewis (1967) have revived the classic question concerning the potential of "autopolyploids" to evolve as successful populations. Perhaps the polyploids in *Perityle* section *Pappothrix* and *Chamaesaracha* (Solanaceae; Powell and Averett, 1967) could be added to the examples presented by the above authors.

There is no evidence that interspecific hybridization has been responsible for the polyploids. In fact, all species of section *Pappothrix* are strictly allopatric and the topography throughout the total range of these species indicates that separation occurred long ago. *Perityle rupestris* var. *albiflora* is known to occur with *P. parryi* (sect. *Perityle*) in the Chisos Mts. of Texas, and fertile hybrids apparently are produced between the two taxa (Powell, 1968a). *Perityle cinerea* cohabits with *P. angustifolia* (sect. *Laphamia*) on a Cretaceous caprock mesa in eastern Pecos Co. No hybrids between the latter two species have been found.

CHEMICAL STUDIES

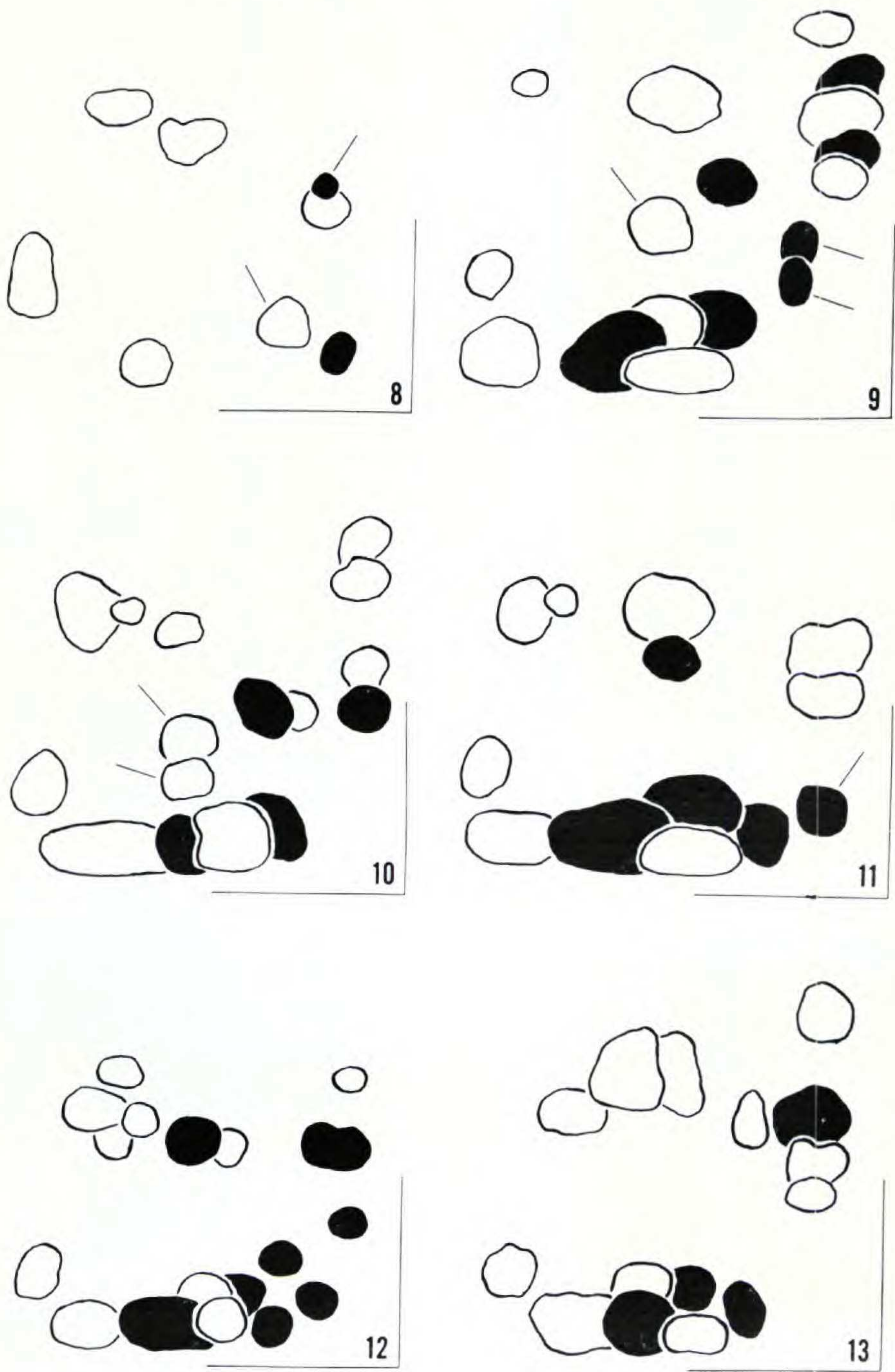
Chemical studies were carried out by the use of 2-dimensional paper chromatography following the techniques reported by Alston and Turner (1963). Distinctions in spots were made in accordance with their different positions on chromatograms and their color variation under ultraviolet light with and without the presence of ammonia vapor.

Figures 1-7. Meiotic chromosomes of some *Perityle* section *Pappothrix* species. Fig. 1. *P. cernua*, $n = 17$, (Sikes & Babcock 328). Fig. 2. *P. cernua*, $n = 17$ II + 1 round fragment denoted by an arrow, (Sikes & Babcock 328). Fig. 3. *P. cernua*, $n = 17$ + 1 round fragment (arrow); late anaphase I showing characteristic behavior of fragment, (Sikes & Babcock 328). Fig. 4. *P. vitreomontana*, $n = 17$, (Sikes 110d). Fig. 5. *P. quinqueflora*, $n = 17$, (Sikes 326b). Fig. 6. *P. rupestris* var. *rupestris*, $n = 68$, (Sikes 91b). Fig. 7. *P. rupestris* var. *albiflora*, $n = 17$. (Powell 1408). All \times ca. 1300 except for Fig. 3 which is \times ca. 1700.

Mere patterns of compounds (probably flavonoids) were employed in the comparison of species, but care was taken to ensure that pattern data were representative of whole populations and not individual plants or seasonal variants (Powell and Tsang, 1966). Each species can be recognized chromatographically by slight differences in patterns (Figs. 8-13). Specific differences are manifested by the consistent presence or absence of unique compounds (oblique lines in Figs. 8-11), and by small combinations of spots which are present in some species but absent in others.

The interpretation of chemical data from *Perityle rupestris* is more difficult because of the occurrence of different patterns for some yellow and white-flowered diploid and polyploid populations of this species (Powell and Tsang, 1966). An understanding of the complex chromatographic variation in *P. rupestris* has not been realized, but after additional testing it is clear that one vexing phenomenon brought out by Powell and Tsang does not hold true in all instances; viz., that diploid white-flowered and polyploid yellow-flowered plants have the ability to produce yellow compounds in much greater abundance than diploid yellow-flowered and polyploid white-flowered plants. A detailed analysis of the chromatographic data obtained for the section *Pappothrix* species will not be possible until a thorough study of the *P. rupestris* complex has been completed. The main purposes of illustrating the chromatographic patterns (Fig. 8-13) are (1) to show the distribution of yellow components among the section *Pappothrix* species, (2) to emphasize the overall similarity of patterns in this subgeneric

Figures 8-13. Chromatographic patterns of the section *Pappothrix* species of *Perityle*. Fig. 8. *P. cernua*. Fig. 9. *P. vitreomontana*. Fig. 10. *P. cinerea*. Fig. 11. *P. quinqueflora*. Fig. 12. *P. rupestris* var. *rupestris* ($n = 17$). Fig. 13. *P. rupestris* var. *albiflora* ($n = 17$). Darkened spots appear yellow under ultra violet light. Spots which appear to be species specific are denoted by oblique straight lines in association with the spots. No species specific or variety specific spots are designated for *P. rupestris* because the variation in patterns produced by diploid-polyploid populations of this taxon is not well understood.



taxon, and (3) to point out the correlated chemical-morphological distinctiveness of *P. cernua* (Fig. 8). Subsequent discussions based largely on morphic evidence (see Phylogenetic Considerations and Taxonomy) suggest a prominent phyletic distance between *P. cernua* and the other four species of section *Pappothrix*.

The copious yellow components (darkened spots) have proven to represent the basis of the tentative chromatographic profile for the whole genus *Perityle*. Not all species of *Perityle* produce the yellow compounds, but those that do not are considered to be relatively removed from the more primitive species on other grounds. Our current knowledge of these compounds is insufficient to permit more than speculation, but this avenue of investigation appears especially promising.

PHYLOGENETIC CONSIDERATIONS

Section *Pappothrix* stands as a monophyletic assemblage of species within the genus *Perityle*. As discussed earlier the primary unifying character is the pappus of numerous bristles. A connection of section *Pappothrix* with section *Laphamia* is seen through *P. vitreomontana*. The pappus of the latter species is reduced to 2-3 main bristles and numerous vestigial nubs (occasionally several other main bristles are evident). This suggests strongly that section *Pappothrix* is ancestral to section *Laphamia* (at least the Texas species), a subject to be discussed further with the taxonomy of section *Laphamia* (Powell, 1969).

No likely extant precursor to section *Pappothrix* has been discovered. Knowledge of such a taxon would be of theoretical importance because it is possible that a *Pappothrix*-like predecessor fostered the sections *Pappothrix* and *Perityle*. As suggested above, a forerunner of the genus *Perityle* possibly had a chromosome number of $n = 18$ or 19 , or maybe even $n = 20$, but at present it appears just as possible that the base number could have been $n = 17$.

It is difficult to predict an ancestral species of section *Pappothrix*, but the progenitor of this phylad must be sought from among *P. cernua*, *P. quinqueflora*, or *P. rupes-*

tris. These three species are basically diploid, yellow-flowered, and produce a well-developed pappus. Of the remaining species, *P. cinerea* is a white-flowered polyploid and *P. vitreomontana* is a white-flowered diploid with a reduced pappus.

The largest number of characters which could be construed as primitive in the section *Pappothrix* line are exhibited by *P. cernua*. These features mainly are solitary, yellow-flowered heads with ca. 150 florets each, large semi-succulent leaves which are glabrous, ca. 35 pappus bristles (compared with 20-30 > 10-14 in other species), and a diploid chromosome number. However, there are factors which might appear to vitiate such a status for *P. cernua*. The species is extremely limited in distribution with a location at the very northwestern periphery of the section *Pappothrix* range. Additionally, chromatographic studies of *P. cernua* have revealed a relatively small quantity of the yellow compounds which are so abundant in other diploid species of this section.

Some factors support the possibility that *Perityle quinqueflora* was the preludial taxon of section *Pappothrix*. Even though the latter species is noted for its numerous reduced heads with 5-6 florets, the leaf morphology is similar to that of *P. cernua* which has what are considered to be the most primitive vegetative features. *Perityle quinqueflora* is a widely distributed diploid species occurring mostly in geologically old limestone areas. Additionally, chromatographic studies have revealed that this species produces yellow compounds in abundance. A few plants in all populations throughout the range of *P. quinqueflora* exhibit heads with 6-8 florets (this is especially true in the population at San Carlos Tunnel in extreme western Jeff Davis Co.), suggesting that reduction in number of florets has been coincident with the evolution of the taxon.

Since plants of *Perityle rupestris* produce heads with 8-12 florets, it is possible to consider this taxon as ancestral to *P. quinqueflora* and perhaps to the other species of section *Pappothrix* as well. However, *P. rupestris* is located mostly in geologically more recent areas than is *P. quinque-*

flora, and the leaves are thinner and more pubescent than are those of the latter species. Even though glabrous conditions might be evolved from pubescent ones in many Composite taxa, this does not seem to have been the case in the derivation of species of section *Pappothrix*. At least in *P. rupestris* a more dense indument seems to be correlated with polyploidy, and the optimum in pubescence of section *Pappothrix* species is seen in the octaploid *P. cinerea*.

When one evaluates the total evidence available, it is apparent that *P. cernua* must be regarded as the ancestral taxon of the section *Pappothrix*. In the first place it would be difficult to visualize how the few, numerous-flowered heads of *P. cernua* could have evolved from a species with numerous 5-12 flowered heads, especially since *P. cernua* is diploid. The determination of the chromosome number of this species was not unequivocal, but certainly the number is $n = 17$ or 18. Regrettably, only one head of buds from this rare species has been available for examination, and it was produced in the greenhouse. I have interpreted the chromosome number to be $n = 17 + 1$ fragment because late anaphase I stages show 17 chromosomes at each pole in many cells, and occasionally 18 at one pole and 17 at the other. A few cells revealed that one chromosome, or portion of a chromosome, was not attached to the spindle apparatus and was left suspended between the poles (Figs. 1-3). Such behavior of chromosome fragments (and univalents) is well known to be associated with reduction in chromosome number. This corresponds with other cytological evidence since there appears to be an aneuploid reduction series in *Perityle* as manifested by several species (Powell, 1968b).

Secondly, the marginal location of *Perityle cernua* within the total section *Pappothrix* range may be construed as enhancing rather than negating a primal position for the taxon. Axelrod (1958) has emphasized that speciation within the general Madro-Tertiary Geoflora was stimulated by adaptation of taxa to drier habitats which came into existence at the margins of deserts. Raven (1964) has discussed catastrophic selection with regard to taxa which become isolated at the peripheries of relatively mesic-xeric habitats.

General principles advanced by both authors appear to fit the proposed evolution of section *Pappothrix* species. Thirdly, it is not yet possible to assess sophisticated conclusions from chemical data. Such data rest ultimately upon the identification of compounds and information regarding their biosynthesis. However, since the obviously more advanced species of section *Pappothrix* (e.g., *Perityle cinerea* and *P. vitreomontana*) produce large amounts of the basic yellow compounds, it is likely that an increased capacity to make the substances is derived. The compounds in question do appear in *P. cernua* but in relatively smaller quantity.

A comparison of present day topography with presumed Late Tertiary geology gives some insight into how the evolution of section *Pappothrix* species could have come about. According to Sellards et al. (1958), a Cretaceous limestone cap extended virtually intact across the Trans-Pecos into New Mexico. With the activity of Tertiary vulcanism and subsequent erosion, many of the rock-bluff potential habitats of section *Pappothrix* species progressively must have become more disjunct. Assuming that the distribution of an ancestral species with vegetative and floral morphology approaching present day *P. cernua* became widespread across an ecologically uniform area before the mountain chains were well separated, the stage would have been set for speciation through geographical isolation. Later erosion could have accounted for more rapid and complete isolation of existing populations such as we see today in the Trans-Pecos. The restriction of section *Pappothrix* species habitats to mountain regions and other prominent land features (such as remnants of limestone caprocks) seems to support such an evolution of taxa.

The broken mountain systems which extend from southern New Mexico through the Trans-Pecos into Mexico apparently were once continuous enough to allow the establishment of a mesophytic montane forest in the higher altitudes, although Wells (1966) has suggested that many of the mesophytic species have never existed in continuum between some of the mountains. All species of section *Pappothrix* occur at various altitudes in these mountains, ex-

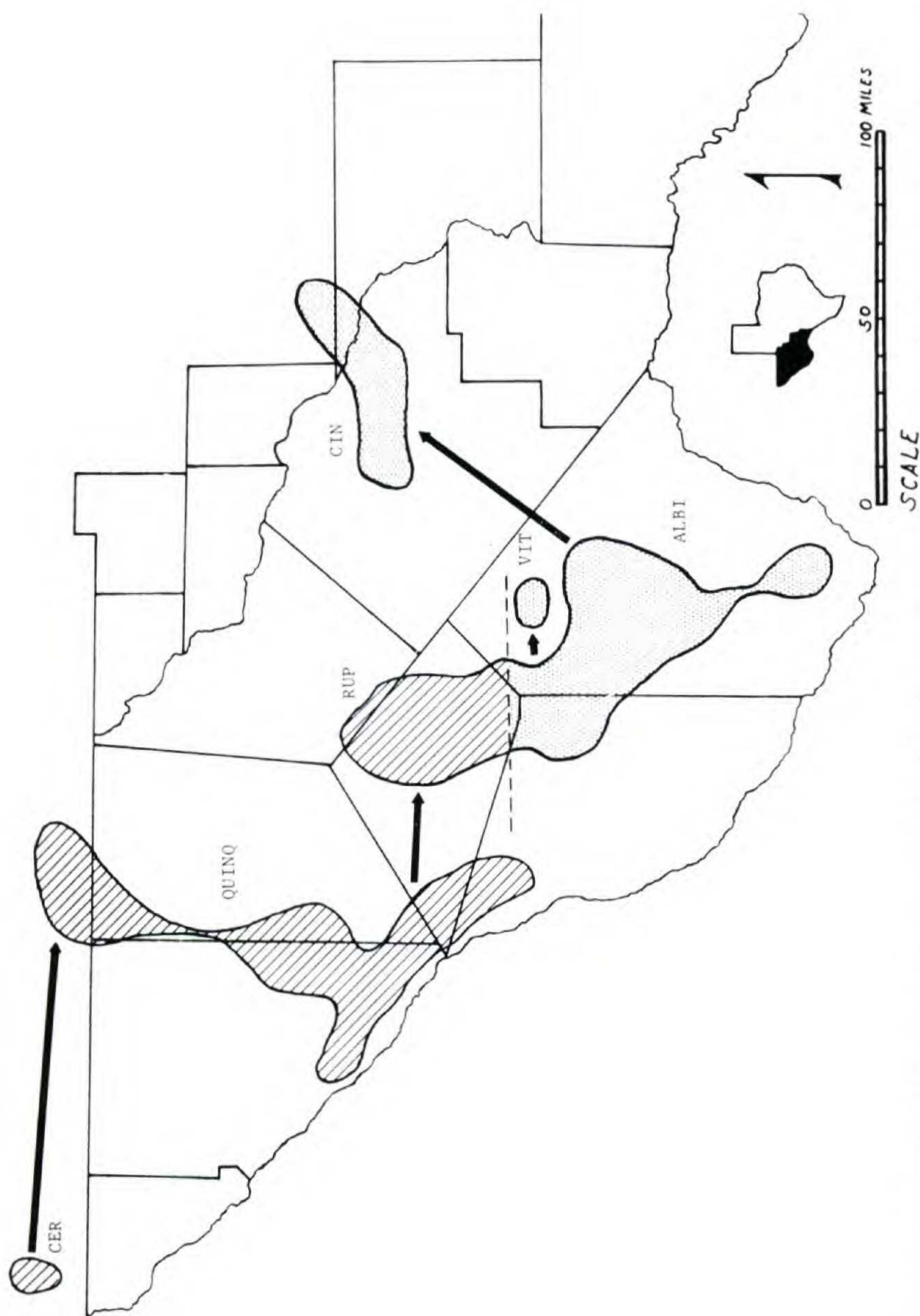


Fig. 14. Supposed evolutionary sequence of *Pappothrix* species. Present day distribution of the yellow-flowered taxa *P. cernua* (CER), *P. quinqueflora* (QUINQ), and *P. rupestris* var. *rupestris* (RUP) is indicated by diagonal lines. Stippled areas designate the ranges of white-flowered *P. rupestris* var. *albiflora* (ALBI), *P. vitreomontana* (VIT), and *P. cinerea* (CIN). The distributional areas of *P. cernua* and *P. vitreomontana* are greatly exaggerated here. Arrows show the probable direction of species development. Relatively speaking, mesic habitats of these species are located in the Organ Mts. (*P. cernua*), Guadalupe Mts. (northern extreme of *P. quinqueflora* range), Davis Mts. (central *P. rupestris* var. *rupestris* range), and Chisos Mts. (southern extreme of *P. rupestris* var. *albiflora* range). All other areas are relatively xeric.

cept *Perityle cinerea*, and it is probable that conditions at least were conducive to the migration of a precursoral taxon. Assuming first of all that section *Pappothrix* represents a northeastern fringe element of the Madro-Tertiary Geoflora, Figure 14 shows how the various section *Pappothrix* species could have arisen after distribution along the mountains in which they are now located from northern into more southern areas. Presumably *Perityle cernua* represents a relictual mesophytic population of ancestral section *Pappothrix* which migrated into the southerly mountains when relatively moist environments prevailed. Since the floral features of *Perityle cernua* (large, solitary heads) differ so markedly from those of *P. quinqueflora* and *P. rupestris*, it is conceivable that a prototype of the latter taxa developed the characteristic smaller, numerous heads long before their divergence as separate species. On the basis of the above postulate, it would follow that *P. cernua* has been isolated much longer than have *P. quinqueflora* and *P. rupestris*. Possibly the latter species gradually became isolated through erosion of their elevated habitats and subsequently becoming adapted to the more xeric habitats in which they now occur. For example, the northernmost population of *P. quinqueflora* in the Guadalupe Mts. resembles *P. cernua* in vegetative habit, and a southernmost population at San Carlos Tunnel resembles *P. rupestris* in the same way. Probably, the San Carlos population of *P. quinqueflora* was most recently isolated from *P. rupestris*. The northernmost populations of *P. rupestris* are more like *P. quinqueflora* vegetatively than the more xerophytic southern populations of this species to the south. It is reasonably certain that yellow-flowered *P. rupestris* preceded the origin of white-flowered *P. rupestris* var. *albiflora*. White-flowered populations are distributed entirely south of the yellow-flowered colonies in somewhat drier habitats (Figure 14).

The white-flowered *Perityle cinerea* and *P. vitreomontana* apparently evolved from offshoots of the white-flowered line arising out of *P. rupestris*. That an ancestral taxon might have given rise to two separate species independently is suggestive of a similar circumstance reported in *Chaenac-*

tis by Kyhos (1965). With these section *Pappothrix* species, however, geographic separation is proposed as the mechanism of initial isolation rather than the aneuploid reduction of chromosome number and structural rearrangements of chromosomes which occurred in *Chaenactis*. *Perityle cinerea* could have originated from a population which migrated into the present Cretaceous caprock area at a time when a more mesic and continuous environment existed throughout the region. Wells (1966) has discovered that pinyon pine was present across the same general territory as recent as Pleistocene. Both *P. cinerea* and *P. vitreomontana* seem to be manifestations of differential adaptation to more xeric habitats. *P. cinerea* has become established as a octaploid species, while *P. vitreomontana* developed as a semi-depauperate diploid species.

If speculations about the ramification of *Perityle cinerea* and *P. vitreomontana* are accurate, an interesting question remains about why their older phylogenetic antecedent did not diverge to a similar degree. Current distribution of the three taxa would suggest that *P. rupestris* var. *albiflora* was never disassociated from *P. rupestris* var. *rupestris*, and their relatively uniform environments, as were *P. cinerea* and *P. vitreomontana*.

Morphological evidences of the relationships projected above can be gleaned from the taxonomic discussions which follow.

TAXONOMY

Perityle sect. *Pappothrix* A. Gray, Pl. Wright. 1: 100. 1852.

Pappothrix (A. Gray) Rydb., N. Amer. Fl. 34: 26. 1914.

TYPE: *Laphamia rupestris* A. Gray.

Plants small suffrutescent perennials, or the stems herbaceous and brittle, growing in crevices of limestone or igneous rock bluffs, glabrous, puberulent, hirsute, pilose, or tomentose-canescens; leaves alternate or opposite, 1.0-4.0 cm long, 0.6-3.0 cm wide, ovate, reniform, or cordate, entire to serrate or serrate-lobed; inflorescence of solitary and erect or nodding heads, or several erect heads, partially obscured by leaves; heads broadly to narrowly campanulate or subcylindric, 0.4-1.4 cm wide; involucre of 2 equal or subequal series; ray flowers absent; disc flowers 5-150; disc corollas yellow or white; style branches linear, tapering to a minutely pubescent point; achenes black, 1.8-

3.0 mm long, oblong to narrowly obconical, partially flattened to sub-cylindric, usually rounded or angled on one or both surfaces, with rather inconspicuous calloused margins, the margins, angles, and surfaces short-pubescent; pappus of (2-7)10-35 slender, unequal bristles, 1.0-3.5 mm long, minutely antrorse-ciliate; base chromosome number, $x = 17$.

Since the taxonomy of the other two sections of *Perityle* will be published separately, a key to all three sections is presented here to facilitate the identification of each sub-generic group.

KEY TO THE SECTIONS

Pappus of (2-7-)10-35 bristles; achenes subcylindrical to partially flattened, margins short-pubescent. sect. *Pappothrix*.

Pappus of 0-2(-3-6) bristles; achenes flattened, margins short-pubescent or profusely ciliate.

Pappus of bristles only (rarely none) or with inconspicuous, vestigial squamellae; achene margins sparsely short-pubescent. sect. *Laphamia*.

Pappus of bristles (rarely none) and a crown of squamellae; achene margins profusely ciliate. sect. *Perityle*.

KEY TO THE SPECIES OF *PERITYLE* SECTION *PAPPO- THRIX*

Heads large, florets ca. 150; corollas yellow; Organ Mts., New Mexico. 1. *P. cernua*.

Heads small, florets 5-16(20); corollas yellow or white.

Florets 5-6(7-8); leaves somewhat lustrous, dark olive-green, subsucculent to coriaceous, typically reniform to subreniform, essentially glabrous to puberulent, rarely hirtellous. 2. *P. quinqueflora*.

Florets (7)8-16(20); leaves lighter green, rather thin, typically ovate, subdeltoid, to subcordate, notably pubescent.

Corollas yellow or white; pappus of 20-30 well-developed bristles; leaves pilose to hirsute; widely distributed in igneous or limestone rocks in Davis Mts., Texas.

Corollas yellow. 3a. *P. rupestris* var. *rupestris*.

Corollas white. 3b. *P. rupestris* var. *albiflora*.

Corollas white; pappus reduced or well-developed; leaves pilose to tomentose-canescens.

Pappus reduced to 2-3(6) main bristles, less often 10-20, including vestigial nubs; leaves pilose; Glass Mts.,

Pappus of 14-20 well-developed bristles; leaves tomentose-canescens; Cretaceous limestone, Pecos, and Upton Counties, Texas. 4. *P. vitreomontana*.

..... 5. *P. cinerea*.



Figure 15. Habit sketch of *Perityle cernua* (Sikes 65); $\times 1$.

1. *Perityle cernua* (Greene) Shinnars, Southw. Nat. 4: 204-209. 1959.

Fig. 15.

Laphamia cernua Greene, Bull. Torr. Bot. Club 25: 122. 1898.

TYPE: NEW MEXICO: DOÑA ANA Co: Organ Mts., at 6500 ft., 4 Sept. 1897, E. O. Wootton 476? (Holotype, ND-G! Isotypes US!).

Pappothrix cernua (Greene) Rydb. N. Amer. Fl. 34: 27. 1914.

Plants 3-6 cm high, closely appressed to rocks, essentially glabrous, dark, lustrous green; leaves alternate or opposite on very short stems, the leaves 2.3-4.0 cm long, 2.0-3.0 cm wide, ovate-reniform to ovate-cordate, the margins unevenly serrate-dentate, essentially glabrous; petioles 0.7-1.5 cm long; inflorescence of solitary and erect or nodding heads often partially obscured by leaves, the peduncles 1.0-1.9 cm long; heads broad-campanulate, 1.0-1.2 cm long, 1.2-1.4 cm wide; receptacle convex, rounded, 3.0-4.0 mm wide, ca. 2.0 mm high; bracts ca. 28, 8-9 mm long, 1.3-1.5 mm wide, linear-lanceolate; disc flowers ca. 150; disc corollas golden yellow, 5.5-6.0 mm long, the tube 1.7-2.0 mm long, minutely glandular-pubescent, the throat narrowly funnel-form, 2.8-3.3 mm long, sparsely glandular-pubescent, the lobes narrow, acute, 0.7-0.8 mm long; achenes 2.1-2.5 mm long, partially flattened; pappus of ca. 35 slender, unequal bristles, 1.2-1.5 (2.0) mm long, minutely antrorse-ciliate; anthers 2.0-2.5 mm long; chromosome number, $n = 17 \text{ II} + 1 \text{ frag.}$

An extremely rare endemic species, known only from the type locality at Dripping Springs Canyon, growing in lime-

stone rock walls, w. side, Organ Mountains, Doña Ana County, New Mexico. Spring-Fall. (Fig. 17).

Representative Specimens:

NEW MEXICO: DOÑA ANA Co: Organ Mts., 29 Aug. 1894, *E. O. Wootton s. n.* (US); n. face of Dripping Springs Canyon, 12 mi. e. of Las Cruces, Organ Mts., *S. Sikes 65* (SRSC): Dripping Springs Canyon, Organ Mts., 10 May 1967, *S. Sikes and C. Babcock 328* (SRSC).

The most anomalous species of section *Pappothrix* is *Perityle cernua*. Easily recognized by its small habit, large, solitary heads, and relatively large leaves, *P. cernua* is not easy to relate to other species. This is true mainly because there are no extant section *Pappothrix* species with such large heads. It is probable that *P. cernua* represents the ancestral species of section *Pappothrix*, exhibiting such primitive characters as yellow flowers, few, large heads with numerous florets, and large, glabrous, thick leaves. Vegetatively, notwithstanding the large heads, *P. cernua* appears closest to *P. quinqueflora*.

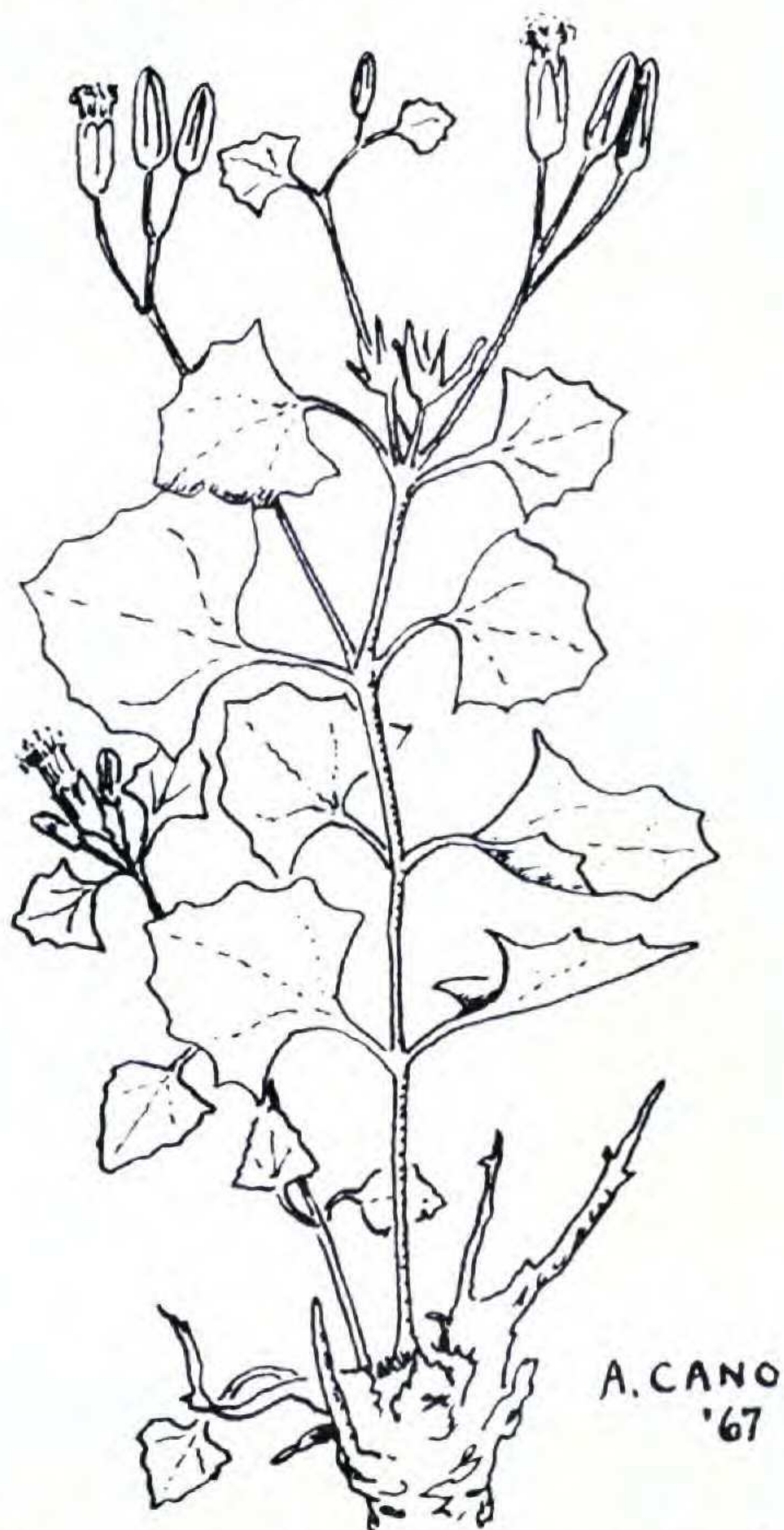


Figure 16. Habit sketch of *Perityle quinqueflora* (Powell 1319);
× 1.

2. **Perityle quinqueflora** (Steyermark) Shinnars, Southw. Nat. 4: 205. 1959. Fig. 16.

Laphamia quinqueflora Steyermark, Ann. Mo. Bot. Garden 19: 392, 393. 1932. TYPE: TEXAS: CULBERSON Co: niches in exposed limestone cliffs, lower McKittrick Canyon, Guadalupe Mts., alt. 1900 m., 20 July 1931, *Moore and Steyermark 3547* (Holotype, GH! Isotypes, CAS! DS! UC! US!).

Pappothrix quinqueflora (Steyermark) Everly, Contrib. Dudley Herb. 3: 375-396. 1947.

Plants 7-30 cm high, densely leafy, essentially glabrous to puberulent; leaves opposite, often becoming alternate above, 1.5-2.5(3.8) cm long, 0.8-2.0(3.3) cm wide, subsucculent to coriaceous, somewhat lustrous, dark olive-green, typically reniform to subreniform, sometimes short-cordate, the margins subentire, dentate-toothed or shallow-lobed, the teeth lobes typically obtuse or rounded but rarely acute, apex obtuse, rounded, or rarely subacute, subcuneate at the base, essentially glabrous to puberulent, rarely hirtellous; petioles 5-8(12) mm long; inflorescence typically of several to many heads in a cluster, borne on rather slender peduncles 2-10(15) mm long; heads cylindrical to very narrowly campanulate, 7-8(9) mm long, 2-3 mm wide, often partially obscured by leaves; receptacle flattened to slightly convex, ca. 1.0 mm wide; involucre of 5-6 bracts in essentially one series, 5-6(9) mm long, (1.0)1.3-1.7 mm wide, strongly keeled; disc florets 5-6(8); disc corollas yellow, 3.8-4.3 (rarely 5.0) mm long, the tube 1.0-1.3 mm long, minutely glandular-pubescent, the throat tubular, 2.0-2.3 (rarely 2.8) mm long, sparsely glandular-pubescent, the lobes acute, reflexed 0.5-1.0 mm long; achenes 1.9-2.0 (rarely 2.5-2.9) mm long, flattened; pappus of 25-30 slender bristles, 1.9-2.5(3.5) mm long, the bristles unequal in length, minutely antrorse-ciliate; anthers 1.5-2.0 mm long; chromosome number, $n = 17$.

Growing extensively in crevices of limestone bluffs (rarely igneous in the Sierra Vieja and Eagle Mts.), in high canyons and caprock. Spring-Fall. (Fig. 17).

Representative Specimens:

NEW MEXICO: EDDY Co: Guadalupe Mts., 12 July 1939, A. L. Hershey 619 (CAS); crevices of limestone rock in canyon to Carlsbad Caverns, 30 May 1965, A. M. Powell 1319 (SRSC); s.w. portion of Dark Canyon, Guadalupe Mts., 1 Sept. 1965, Powell & Sikes 1379 (SRSC). CULBERSON Co: Pine Canyon, Guadalupe Mts., 20 June 1964, D. S. Correll & C. Hanson 29791 (LL); South McKittrick Canyon, 2 July 1958, Correll & I. M. Johnston 19177 (LL); Beach Mts., 8 mi. n. of Van Horn, 3 June 1938, H. C. Cutler 1978 (CAS); South McKittrick Canyon, 25 Aug. 1950, W. V. Fischer s.n. (UC); South McKittrick Canyon, 11 July 1948, L. C. Hinckley 4467 (SRSC); upper McKittrick Canyon, 21 June 1947, F. G. Meyer & L. E. Meyer 2178 (UC); between

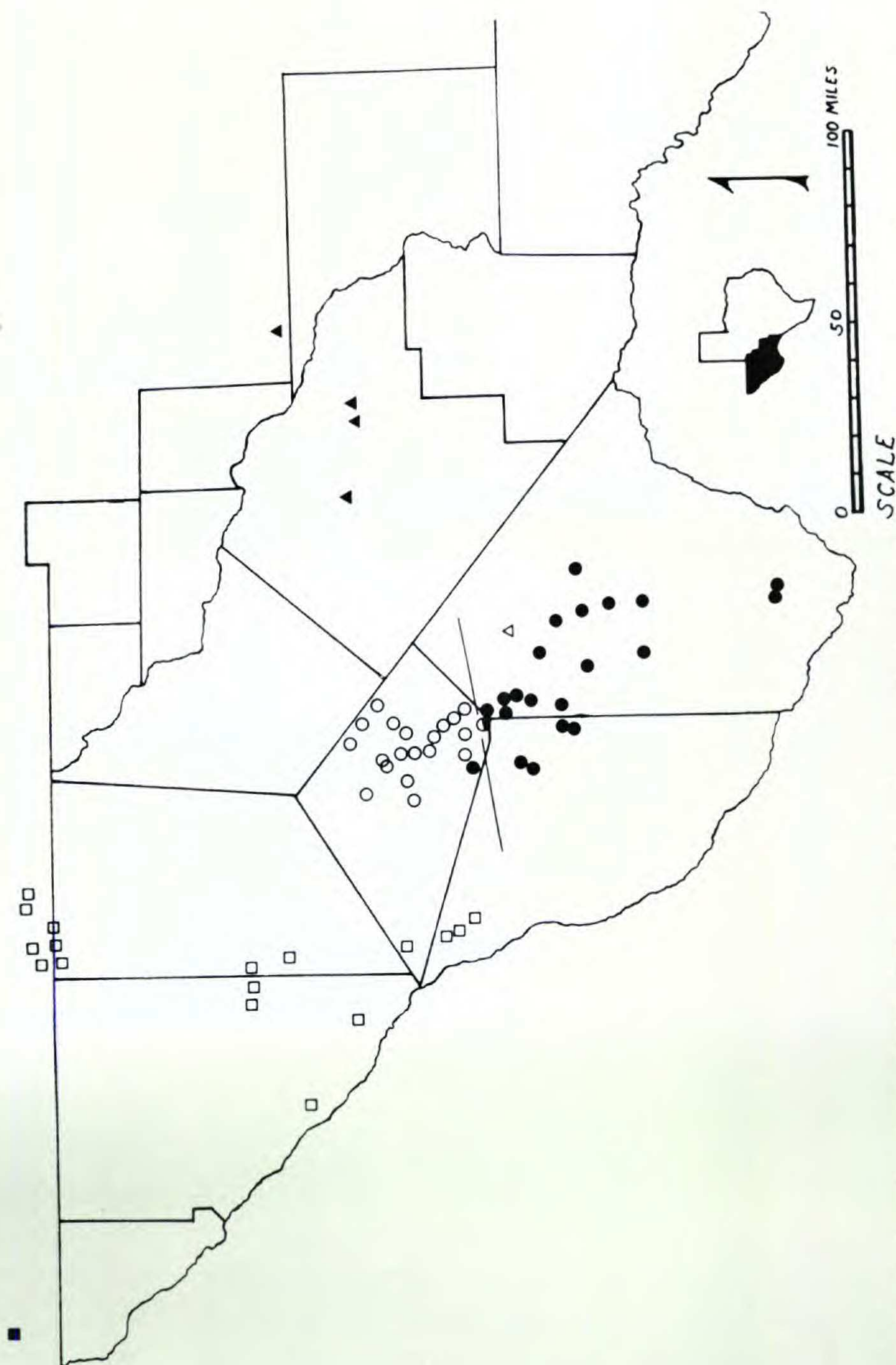


Figure 17. Distribution of *Perityle* section *Pappothrix* species: *P. cernua* (closed square, Organ Mts., N. M.); *P. quinqueflora* (open squares); *P. rupestris* var. *rupestris* (open circles); *P. rupestris* var. *albiflora* (closed circles); *P. vitreomontana* (open triangle); *P. cinerea* (closed triangle). A solid line emphasizes the discontinuity of the varieties of *P. rupestris*; the location of a sympatric population is denoted by a half-closed circle.

South & North McKittrick Canyons, 15 July 1945, *R. McVaugh* 7398 (LL, SMU); Smith Canyon, Guadalupe Mts., 17 July 1945, *R. McVaugh* 7418 (LL, SMU); South McKittrick Canyon, 4 July 1964, *A. M. Powell, B. Calvert, & P. Tsang* 1246 (SRSC); Victoria Canyon, Sierra Diablo, 10 Aug. 1946, *L. H. Shinnars* 8865 (SMU, TEX); Pine Springs Canyon, Guadalupe Mts., 15 Aug. 1946, *Shinnars* 9062 (SMU); McKittrick Canyon, 15-17 Aug. 1924, *P. C. Standley* 40562 (US); upper Pine Springs Canyon, 15 Sept. 1948, *B. L. Turner & B. H. Warnock* 123 (LL, SMU, SRSC); Smith Canyon, 10 July 1949, *Turner and Warnock* 1265 (SMU, SRSC); McKittrick Canyon, 30 Aug. 1950, *Warnock* 9456 (LL, SRSC); Victoria Canyon, Diablo Mts., 11 July 1956, *Warnock* 14091 (LL, SRSC); South McKittrick Canyon, 11 Sept. 1962, *Warnock* 20407 (SRSC); South McKittrick Canyon, 18 May 1958, *Warnock & M. C. Johnston* 16529 (SRSC); lower Pipe Line Canyon, 5 July 1958, *Warnock & Johnston* 16589 (SRSC); North McKittrick Canyon, 4 Aug. 1962, *Warnock & T. Rogers* 18864 (SRSC); Pine Top Mt., 28-29 July 1952, *G. L. Webster* 4578 (SRSC); Guadalupe Mts., 15 Aug. 1916, *M. S. Young s.n.* (TEX); Guadalupe Mts., 2 Sept. 1916, *M. S. Young s.n.* (TEX, SRSC). HUDSPETH Co: Quitman Canyon, Quitman Mts., 13 Oct. 1952, *D. S. Correll* 15065 (LL); s. Sierra Diablo Plateau, 9 Sept. 1961, *Correll & Johnston* 24362 (LL); upper limestone slopes, Victoria Canyon, 10 July 1945, *R. McVaugh* 7359 (LL, SMU); Van Horn, 4 Sept. 1925, *B. C. Tharp* 3818 (TEX); head of Victoria Canyon, 18 Aug. 1953, *Warnock* 11495 (SRSC); s.e. of Old Love Ranch, Eagle Mts., 22 Aug. 1946, *U. T. Waterfall* 6684 (NY). JEFF DAVIS Co: San Carlos Tunnel, 22 July 1967, *Powell & Sikes* 1536 (SRSC); ca. 20 mi. w. of FM 2017, San Carlos Tunnel, 11 May 1967, *Sikes & Babcock* 326 (SRSC). PRESIDIO Co: Bracks Canyon, Sierra Tierra Vieja, 11 June 1941, *L. C. Hinckley* 1675 (SMU, TEX, US); near rimrock, Sierra Tierra Vieja, 4 Oct. 1941, *Hinckley* 2185 (LL, NY); Vieja Pass, Vieja Mts., 3 Aug. 1960, *Warnock* 19600 (SRSC).

It is clear that *Perityle quinqueflora* is most closely related to *P. rupestris*. In fact, the several collections from Sierra Tierra Vieja (Jeff Davis Co. and Presidio Co.) are difficult to distinguish from *P. rupestris*. Normally *P. quinqueflora* is readily distinguished from *P. rupestris* by 5(6) flowered heads, 5(6) involucral bracts, rather fleshy, dark green, subglabrous leaves with margins varying from subentire to serrate-lobed, and habitat mainly in limestone rock. The Sierra Vieja collections at San Carlos Tunnel approach *P. rupestris* by exhibiting 5-7(8) florets and bracts per head, and thinner, lighter green, hirtellous leaves with deep serrations of the leaf margins. Even though the Sierra Vieja population closes the morphological gap between these

two taxa, there is no evidence of intergradation. Geographically *P. quinqueflora* and *P. rupestris* remain well separated (Fig. 17).

It is interesting to speculate about the phylogeny of these related entities. *Perityle quinqueflora* features several reduced characters, especially the 5-membered heads and essentially glabrous habit, and could thus be viewed as derived from *P. rupestris*. However, the former species is distributed in the geologically older areas, for the most part, and is known only as a diploid. *Perityle rupestris* on the other hand, at least the yellow-flowered variety, occupies the geologically more recent tertiary igneous intrusive and extrusive formations in Jeff Davis Co., and occurs in diploid and polyploid forms. The white-flowered variety of *P. rupestris* inhabits both limestone and igneous formations.

As discussed above, most evidence concerning the relationship of *P. quinqueflora* and *P. rupestris* seems to indicate an evolution of both species from a widespread ancestor much like *P. cernua*. Hypothetically, two large populations could have been isolated geographically in recent geological history when their relatively continuous rock-bluff habitats were eroded away. Once they were separated the populations would have been free to follow their independent evolutionary paths. It is possible that a fluctuating Pleistocene environment could have allowed secondary sympatry after initial isolation if erosion of intermediate habitats was not complete. There is no evidence for the latter unless one considers the somewhat morphologically intermediate colony of *P. quinqueflora* at San Carlos Tunnel to have resulted from hybridization with *P. rupestris*. At this time it appears feasible to interpret the San Carlos population as one which has been most recently segregated from *P. rupestris*.

3a. *Perityle rupestris* (Gray) Shinnars var. *rupestris*, Southw. Nat. 4: 204-209. 1959. Fig. 18.

Laphamia rupestris Gray, Pl. Wright. 1: 100. 1852. TYPE: TEXAS: JEFF DAVIS CO: crevices of rocks, on mountains, in the Pass of the Limpia, Aug. 1849, Charles Wright 300

(Holotype, GH! Isotypes, GH! NY! US! Photograph, DS!).

Pappothrix rupestris (Gray) Rydb. N. Amer. Fl. 34: 26. 1914.

Plants 6-20(35) cm high, puberulent, pilose, or hirsute, profusely branched and leafy; leaves opposite or alternate, usually alternate, 1.0-2.5(3.5) cm long, 0.7-1.7(3.0) cm wide, ovate to broadly so, subdeltoid, subcordate, or rarely subreniform, the margins irregularly serrate or serrate-lobed, the serrations or lobes acute (rarely obtuse), pilose, hirsute, or rarely puberulent; petioles 0.3-1.3 cm long; inflorescence of solitary heads or small, loose clusters, heads borne on rather short peduncles, often partially obscured by leaves; receptacles flattened to slightly convex, 1.0-1.5 mm wide; heads subcylindric, subfunneliform, or narrowly campanulate, 6-8 mm long, 3-5 mm wide; bracts 8-10, 4-7 mm long, 1-2 mm wide, typically oblong to oblong-lanceolate, keeled; disc flowers (7) 8-12; disc corollas yellow, 4.0-5.2 mm long, the tube 1.0-1.3 mm long, minutely glandular-pubescent, the throat tubular to subfunneliform, 2.2-3.0 mm long, the lobes acute, 1.0-1.3 mm long; achenes (1.8) 2.0-2.5 mm long, subtruncate or tapering toward the base, flattened (rarely nearly cylindric); pappus of 20-30 slender, unequal, bristles, 2.0-3.0(3.5) mm long; anthers 2.0-2.5 mm long; chromosome numbers, $n = 17, 34, 68$.

An extremely variable taxon, common in crevices of igneous boulders and bluffs, from ca. 10 mi. north of Alpine

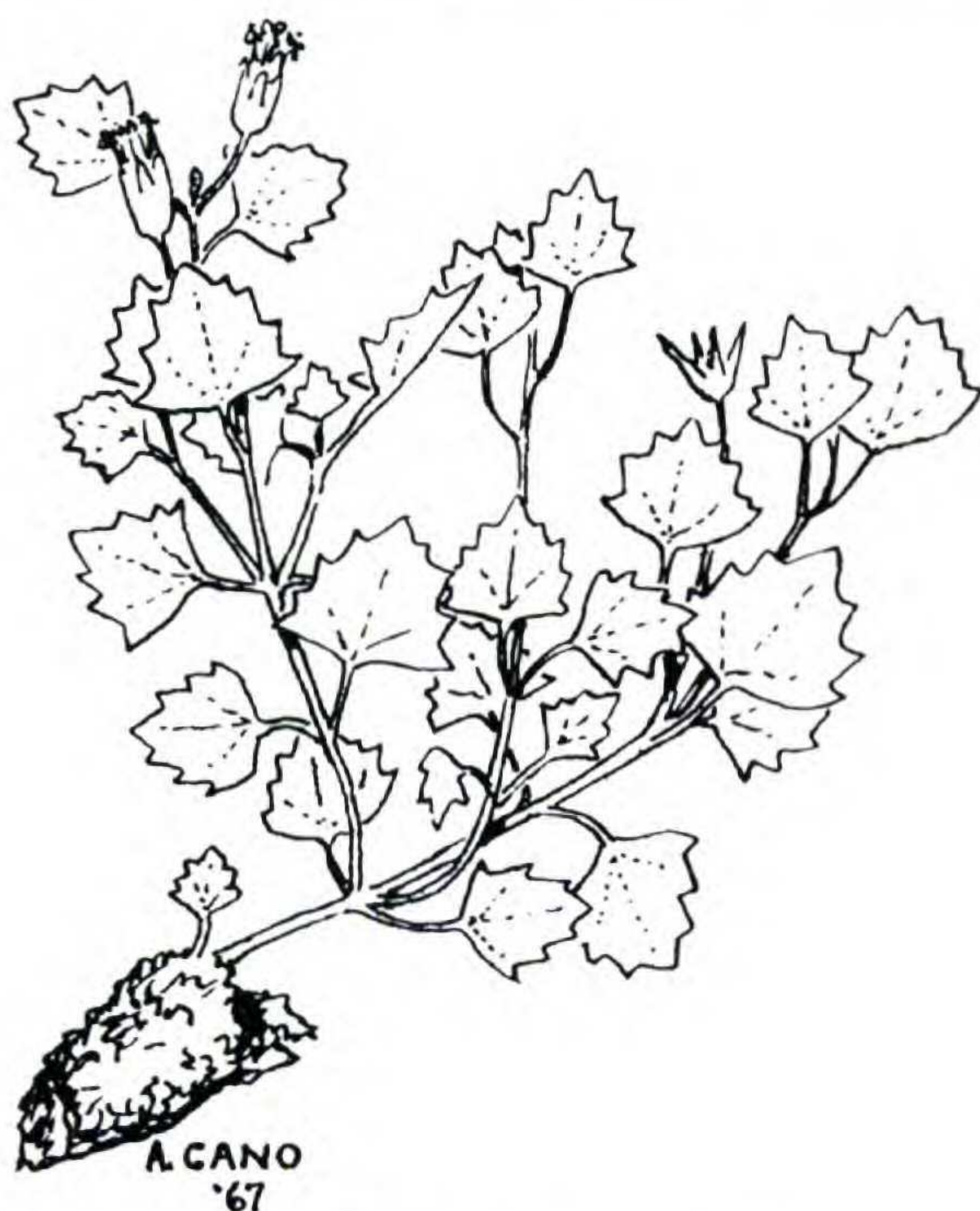


Figure 18. Habit sketch of *Perityle rupestris* var. *rupestris* (Powell 1228); $\times 1$.

throughout Jeff Davis County and probably north Presidio County. Spring-Fall. (Fig. 17).

No mention of flower color was made in Gray's original description of *Laphamia rupestris*, but the morphology of the type specimens and Wright's collection site indicate that this is a member of the yellow-flowered variety.

Representative Specimens:

TEXAS: JEFF DAVIS Co: e. slope, Haystack Mt., 6050 ft., 27 May 1959, *T. J. Allen* 353 (SRSC); 10 mi. s.e. of Ft. Davis, 28 April 1947, *V. L. Cory* 53568 (NY, SMU); Fort Davis, 19 Sept. 1920, *W. W. Eggleston* 17425 (NY, US); Fort Davis, 20 Sept. 1920, *Eggleston* 17474 (NY, US); rocky hillside back of old Ft. Davis, 9-12 July 1921, *R. S. Ferris & C. D. Duncan* 2683 (DS); 12 mi. n. of Alpine, 18 Oct. 1933, *H. T. Fletcher* 1482 (SRSC); Goat Canyon, Mt. Livermore, 7 Sept. 1935, *L. C. Hinckley* s.n. (TEX); n. side of Timber Mt., near Madera Springs, 24 July 1949, *L. C. Hinckley & L. Hinckley* 193 (SMU, SRSC); Limpia Canyon at Wild Rose Pass, 11 Sept. 1949, *Hinckley & Hinckley* 338 (SRSC); ridge s. of Mt. Livermore, 21 Aug. 1935, *Hinckley* 356 (LL); Mt. Livermore, Aug., 1935, *Hinckley* 507 (SRSC); Limpia Canyon near Ft. Davis, 8 Oct. 1944, *Hinckley* 338½ (SRSC); igneous rock above old Ft. Davis, 6 Nov. 1958, *M. C. Johnston* 3578 (SRSC); igneous rock, 18 mi. n. of Alpine, 6 Nov. 1958, *Johnston* 3589 (SRSC); 15 mi. n. e. of Ft. Davis, canyon e. of Limpia Creek, 24 May 1949, *R. McVaugh* 10626 (SRSC, US); Little Aguja Canyon, 12 June 1931, *J. A. Moore & J. A. Steyermark* 3041 (CAS, DS, NY, UC, US); clefts and ledges of porphyritic rocks, Davis Mts., 7 Oct. 1926, *E. J. Palmer* 32029 (TEX); crevices in basaltritic rocks, on the Limpia, *C. C. Parry* s.n. (NY); ca. 2 mi. n. of Ft. Davis along Limpia Creek, 6 June 1964, *A. M. Powell & B. Calvert* 1228 (SRSC); ca. 17 mi. n. of Alpine along Musquiz Creek, 6 June 1964, *Powell & Calvert* 1229 (SRSC); large igneous boulders, 16 mi. n. of Alpine, 14 May 1965, *A. M. Powell & P. R. Powell* 1316 (SRSC); 11 mi. n. of Marfa, 19 Aug. 1967, *Powell* 1550 (SRSC); 10 mi. n. of Alpine, near Mitre Peak, 5 June 1965, *S. Sikes* 4a (SRSC); Davis Mt. State Park, 3 Sept. 1965, *Sikes* 15 (SRSC); 6 mi. n. w. of Ft. Davis, 3 Sept. 1965, *Sikes* 15, 16 (SRSC); Madera Canyon, n. w. of Ft. Davis, 3 Sept. 1965, *Sikes* 17, 18, 19 (SRSC); Boy Scout Camp n. of Ft. Davis, 30 Sept. 1965, *Sikes* 33 (SRSC); Timber Mt., n. of Ft. Davis, 5 June 1966, *Sikes* 45 (SRSC); 13 mi. s. of Toyahvale, 28 Aug. 1966, *Sikes* 91 (SRSC); rock crevices, Fern Canyon, 20 Oct. 1945, *O. Sperry* T1322 (US); Fern Canyon, Aug. 1932, *T. L. Steiger* 954 (NY); lower Limpia Canyon, 9 May 1937, *B. H. Warnock* T80 (TEX, US); Musquiz Canyon, 16 mi. n. of Alpine, 19 June 1947, *Warnock* 6158 (SRSC); n. slopes of Timber Mt. above Madera Springs, 20 July 1947, *Warnock* 6493

(SRSC); upper Madera Canyon, Mt. Livermore, 11 Sept. 1947, *Warnock & Hinckley 7458* (SRSC); upper Madera Canyon, 25 Oct. 1947, *Warnock 7619* (SRSC); Wild Rose Pass, Limpia Canyon, 24 May 1949, *Warnock & McVaugh 8649* (SRSC); n. side Timber Mt., 14 May 1950, *Warnock & N. Tallant 9058* (SRSC); 12 mi. n. of Alpine, 13 Sept. 1963, *Warnock & Powell 19289* (SRSC); 12 mi. n. of Alpine, 11 Sept. 1962, *Warnock 20404* (SRSC); 15 mi. n. of Alpine, upper Rose Canyon, 1 July 1940, *Warnock 20909* (TEX); 20 mi. s. s. e. of Kent, 31 July 1943, *U. T. Waterfall 5406* (CAS, NY); Davis Mt. Park, 23 June 1941, *E. Whitehouse 12129* (SMU); Mt. Livermore, 14 Aug. 1914, *M. S. Young s. n.* (TEX).

- 3b. *Perityle rupestris* (Gray) Shinnars var. **albiflora** Powell, *Sida* 3: 180. 1967. TYPE: TEXAS: BREWSTER Co: in crevices of igneous bluffs, ca. 3 mi. w. of Alpine in Tronto Pass, 3 June 1965, *A. M. Powell & S. Sikes 1320* (Holotype, SRSC; isotypes, GH, SMU, TEX, US).

Disc corollas white; disc florets 8-18; achenes 1.8-2.5 mm. long; pappus bristles 18-25, 1.0-2.0 mm. long; chromosome numbers, $n = 17, 34, 85$.

A variable taxon, common in crevices of igneous and limestone bluffs and boulders, from ca. 10 mi. n. of Alpine, south throughout Brewster County, extreme south Jeff Davis County, and eastern Presidio County.

This variety is distinguished by white disc corollas, smaller leaves in most populations, tendency for more florets per head, pappus bristles mostly as long as or shorter than the achenes, and geographic distribution (Fig. 17).

Representative Specimens:

TEXAS: BREWSTER Co: ca. 15 mi. s. e. of Marathon, 13 Sept. 1961, *D. S. Correll & M. C. Johnston 24577* (LL); Pena Blanca Mts., 6 mi. e. of Hwy. 385, 30 Sept. 1962, *Correll & H. B. Correll 26109* (LL); Pine Canyon, Chisos Mts., 17 June 1963, *Correll & D. C. Wasshausen 27867* (LL); vicinity of Alpine, 7 June 1926, *D. Demaree & E. J. Palmer 104* (SMU); n. slope, Cathedral Mt., 21 July 1960, *L. Doyles & B. Jobs 71* (SRSC); Lizzard Mt., 2 mi. w. of Alpine, 21 Sept. 1934, *H. T. Fletcher 144* (SRSC); Lizzard Mt., 10 Sept. 1929, *Fletcher 1384* (SRSC); s. end of Del Norte Mts., 6 Sept. 1947, *L. C. Hinckley & F. M. Churchill 4112* (SMU, US); Alpine, 3 Oct. 1930, *R. Hughes 12* (NY); upper slopes Cathedral Mts., 26 June 1959, *J. Jackson 130* (SRSC); ca. 16 mi. s. e. of Marathon, 13 July 1964, *A. M. Powell & B. Calvert 1252* (SRSC); Tronto Pass, ca. 3 mi. w. of Alpine, 3 June 1965, *Powell & S. Sikes 1320* (SRSC); 17 mi. s. of Marathon, 31 May 1966, *Powell, T. Watson, & Sikes 1408* (SRSC); Hidden Valley near Alpine, 20 June 1941, *R. Rose-Innes & B. Moon*

1261 (TEX); Sunny Glen, 4 mi. w. of Alpine, 4 June 1965, *Sikes 1* (SRSC); 6 mi. n. of Alpine, 5 June 1965, *Sikes 2* (SRSC); 12 mi. s. of Marathon, 4 Sept. 1965, *Sikes 20, 21, 22* (SRSC); n. side of Cathedral Mt., 23 Sept. 1965, *Sikes 29* (SRSC); Basin, Chisos Mts., 26 Sept. 1965, *Sikes 31* (SRSC); Doubtful Canyon, 12 mi. s. e. of Alpine, 2 Sept. 1966, *Sikes 93* (SRSC); s. slopes, Cathedral Mt., 21 July 1960, *M. Snowden & R. Rice 374* (SRSC); Paradise Canyon, 22 Sept. 1935, *O. E. Sperry T325* (LL, SRSC, US); Alpine, May, 1932, *T. L. Steiger 1043* (NY); Jackson Ranch, near Alpine, 13 Aug. 1938, *B. H. Warnock T513* (US); Bluff Cave, 6 mi. s. w. of Alpine, 24 June 1940, *Warnock W907* (TEX); 6 mi. n. w. of Alpine, 17 May 1947, *Warnock 5580* (LL, SMU, SRSC, TEX); 16 mi. s. of Marathon, 29 June 1947, *Warnock 6127* (SRSC, TEX); Doubtful Canyon, 25 mi. s. of Alpine, 18 Sept. 1947, *Warnock & Hinckley 7527* (SRSC); Doubtful Canyon, 18 Sept. 1947, *Warnock & Hinckley 7535* (SMU, SRSC); Doubtful Canyon, 11 July 1948, *Warnock 7983* (LL, SMU, SRSC); upper Pine Canyon, Chisos Mts. 1 Aug. 1950, *Warnock 9179* (SRSC); base of Bailey Peak, Chisos Mts., 6 Sept. 1950, *Warnock 9593* (SRSC); 18 mi. s. of Marathon, 17 June 1964, *Warnock 20419* (SRSC); 3 mi. w. of Alpine, 15 Sept. 1964, *Warnock 20491* (SRSC); 20 mi. s. e. of Marathon, 29 Sept. 1964, *Warnock 20501* (SRSC); Pena Blanco Springs, 9 Oct. 1964, *Warnock 20548* (SRSC). JEFF DAVIS Co: 10 mi. n. of Alpine, near Mitre Peak, 5 June 1965, *Sikes 4b* (SRSC). PRESIDIO Co: e. slope, Goat Mt., 1 Sept. 1959, *L. Campsey 315* (SRSC); e. slope, Goat Mt., 22 Aug. 1959, *Campsey 1060* (SRSC); below San Estaban Lake, 12 mi. s. of Marfa, 18 Aug. 1940, *Hinckley 1296* (LL, NY); Alamito Creek, below San Estaban Lake, 26 June 1964, *Powell 1237* (SRSC); bluffs, s. w. edge of Marfa Flats, ca. 13 mi. s. of Marfa, 26 June 1964, *Powell 1238* (SRSC); n. w. side of Goat Mt., 23 Sept. 1965, *Sikes 30* (SRSC); s. side of Goat Mt., 11 June 1966, *Sikes 48* (SRSC); San Estaban Canyon, 28 May 1957, *Warnock & W. D. McBride 14487* (LL, SRSC); below San Estaban Lake, 24 June 1964, *Warnock 20411* (SRSC); Goat Mt., 5 Aug. 1941, *Warnock 21338* (SMU, TEX).

Perityle rupestris shares its closest relationship with *P. quinqueflora*. This subject is discussed further in connection with the latter species. The primary distinguishing features of *P. rupestris* var. *rupestris* include (7) 8-12 flowered heads, and serrate-lobed leaves which are pilose to hirsute. *Perityle rupestris* var. *albiflora* is readily delimited by its white flowers.

As a relatively wide-ranging species *P. rupestris* is one of the most variable in the genus, being comprised of many populational and cytological entities. In distribution the species extends from the north edge of the Davis Mts. south

to the Chisos Mts. in Brewster Co., and eastern Presidio Co. Practically every disjunct mountain segment in this general area (those with rock bluffs) serves as the habitat for a population of *P. rupestris* which is different either in ploidy level or a few morphic features. However, geographically and morphologically only two varieties seem worthy of recognition. No mixed populations of yellow and white-flowered plants have been found on either side of the imaginary line seen in Figure 19. One small sympatric colony of predominately white-flowered plants was discovered in an intermediate locality which is denoted in Figure 19 along the separatory imaginary line.

At least three other populations of *Perityle rupestris* are reasonably distinct morphologically, cytologically, and geographically, but at the present, it seems that the differences are not sufficient to allow for formal recognition. Locations of the three populations are noted in Figure 19, and examples of each are as follows:

- 1) *Sikes 45*, Jeff Davis Co., n. slopes of Timber Mt. above Madera Springs; flowers yellow, large heads, large, subreniform leaves, chromosome number, $n = \text{ca. } 34$.
- 2) *Powell 1408*, Brewster Co., 17 mi. s. of Marathon; flowers white, restricted to Caballos Novaculite exposures in the Marathon Basin, chromosome number, $n = 17$.
- 3) *Powell 1237*, Presidio Co., 9 mi. s. of Marfa, below San Estaban Dam; flowers white, leaves large, chromosome number, $n = 34$.

Several other polyploid populations of both yellow and white-flowered varieties have been discovered (Table I), but these do not deviate notably from the typical morphology of their respective varieties. Many individual plants of most populations have been checked for their chromosome number, and the ploidy level has been shown to be consistent in each population, or at least in each cluster of plants examined. However, two qualified exceptions to the latter condition have been detected. In Madera Canyon of Jeff Davis Co., tetraploids ($n = 34$) and diploids ($n = 17$)

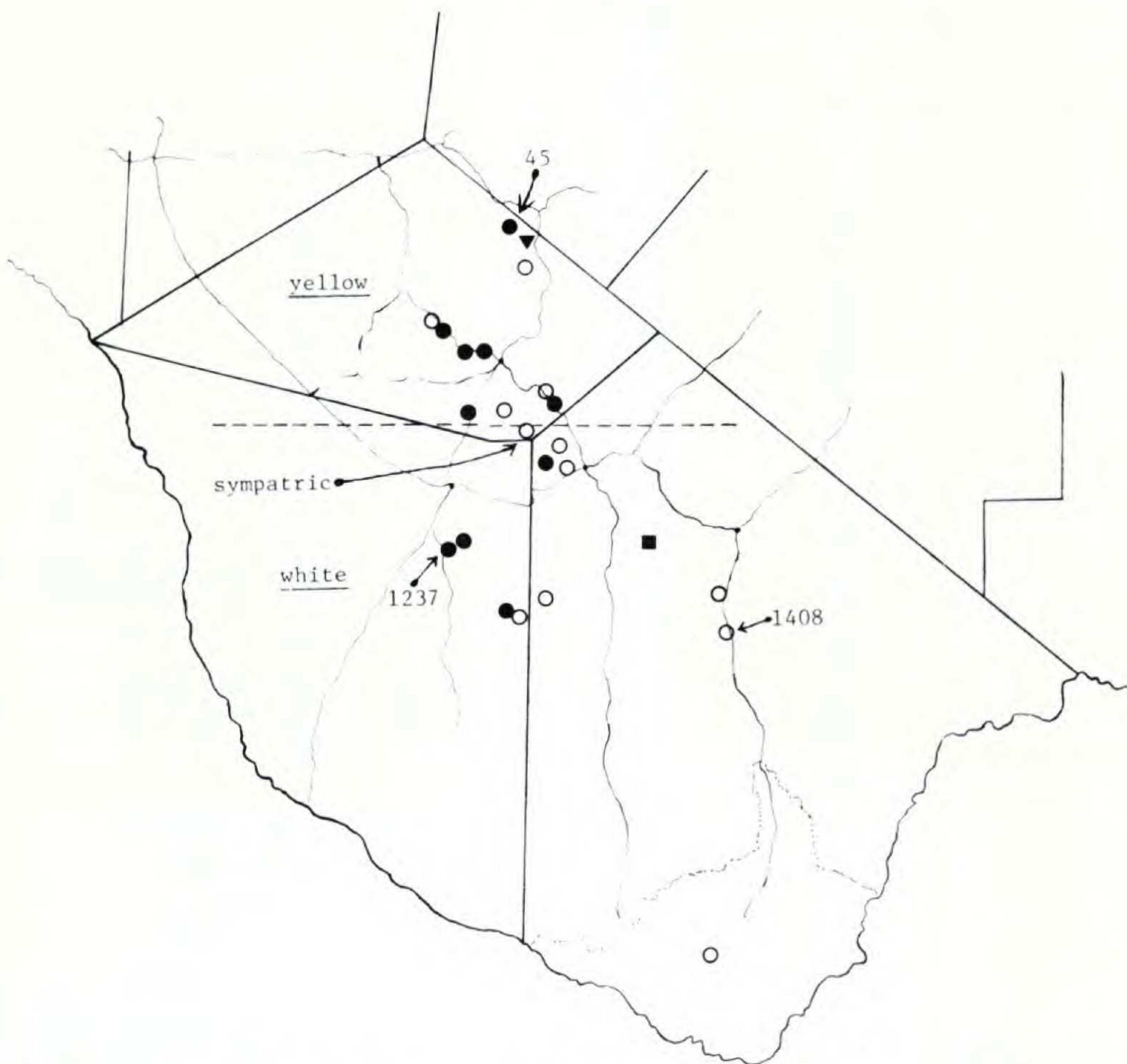


Figure 19. Distribution of diploid and polyploid populations of *Perityle rupestris*: Open circles ($n = 17$); closed circles ($n = 34$); triangle ($n = 68$); and square ($n = 85$). The broken line designates a uniform disjunction of yellow-flowered populations (*P. rupestris* var. *rupestris*) to the north and white-flowered populations (*P. rupestris* var. *albiflora*) to the south. An arrow points to the intermediate location of a sympatric colony of predominately white-flowered plants. Locations of three populations with cytological and/or slight morphological differences from typical *P. rupestris* are denoted by voucher collection numbers and arrows.

were collected about 20 feet apart. On Goat Mountain in Presidio Co., tetraploids were collected on the northwest side and diploids on the south side, and it is likely that plants with both ploidy levels are mixed at some point along the west side of the mountain.

There seems to be no pattern for the evolution of polyploid populations of *P. rupestris* (Fig. 19). It is clear, however,

that once polyploids become established they are successful, even to the exclusion of diploids or other ploidy levels.

No direct evidence has been accrued to elucidate the origin of polyploids in *P. rupestris*. The similar morphology of diploids and polyploids seems to justify speculation that all the polyploids in this species have arisen through autoploidy or perhaps segmental allopolyploidy in the sense of Stebbins (1950). There is no indication that other species of section *Pappothrix* have contributed to an allopolyploid origin of any polyploid populations of *P. rupestris* even though preliminary interspecific hybridization experiments (Powell, 1968a) with diploid species have shown that there is no stringent reproductive isolation between species.

Reasonable conjecture would lead one to believe that populational isolation of a wide-spread *P. rupestris* began with the erosion of semi-continuous mountain systems in the Trans-Pecos region of Texas. A cursory examination of the present discontinuous topography and ecology (mainly habitat in crevices of rocks) in the Trans-Pecos indicates that interspecific and even large-scale interpopulational outcrossing of *P. rupestris* populations was probably precluded. This is substantiated by both the allopatric distribution of the extant species of section *Pappothrix*, and in particular by the allopatry of the various different populations of *P. rupestris*.

The anomalous populations of *P. rupestris* are being studied chromatographically, with some interesting results (Powell and Tsang, 1966). A comprehensive systematic study of this diploid and polyploid complex is in progress.

4. *Perityle vitreomontana* Warnock, Southw. Nat. 12 (4): 475-476. 1967.

TYPE: TEXAS: BREWSTER Co: limestone bluffs, w. slopes of Old Blue, Glass Mountains, ca. 4500 ft., 22 Sept. 1963, B. H. Warnock and A. M. Powell 19111 (Holotype, SRSC! Isotype, TEX!).

Plants 3-10 cm high, pilose, densely leafy; leaves opposite, becoming alternate above, 0.7-1.0 (1.3) cm long, 0.5-0.8 (1.2) cm wide, ovate to ovate-deltoid, the margins obtuse-serrate to incised-lobed, rarely laciniate, typically obtuse, rarely subacute at the apex, sub-

truncate to subacute at the base, pilose, strongly veined; petioles 2-4 mm long; inflorescence typically of loosely clustered heads, rarely solitary, borne on short peduncles, (0.1) 0.2-0.3 (0.8) cm long; heads narrowly campanulate, 6-7 mm long, 3-4 mm wide, often mostly obscured by leaves; receptacle essentially flattened to slightly convex, 1-2 mm wide; bracts (9) 10-12, 4-5 mm long, 0.8-1.0 mm wide, obscurely keeled; disc flowers 11-16; disc corollas white, 4.2-4.5 mm long, the tube 0.8-1.0 mm long, minutely glandular-pubescent, the throat tubular, ca 2.5 mm long, sparsely glandular-pubescent, the lobes narrow, acute, reflexed, 0.8-1.0 mm long; achenes 1.9-2.0 mm long, flattened, typically truncate at base and apex; pappus typically of 2-(3) very slender bristles, 1.2-2.0 mm long, often with 3-6 bristles, most shorter than the main 2, rarely with 10-20 short to vestigial bristles and nubs, the bristles minutely antrorse-ciliate; anthers ca. 2.0 mm long; chromosome number, $n = 17$.

A rare edemic found only on limestone bluffs in the Glass Mountains, north and north-west side, eastern Brewster County (Fig. 17).

Representative Specimens:

TEXAS: BREWSTER Co: limestone bluffs, n. side, Glass Mts., S. Sikes 110 (SRSC); on Baldy Peak, Glass Mts., 13 July 1940, B. H. Warnock W247 (SRSC, TEX, UC); w. slopes of Gilliland Peak, Glass Mts., 5400 ft., 29 Aug. 1947, B. H. Warnock 6953 (SRSC); w. slopes of Old Blue, Glass Mts., 4700 ft., 27 July 1957, Warnock and W. D. McBride 15663 (LL, SRSC); near top of Old Blue, Glass Mts., 6500 ft., 15 Aug. 1962, Warnock 20405 (SRSC); Old Blue, Glass Mts., 5000 ft., 18 June 1964, Warnock 20412 (SRSC).

This remarkable species exhibits a superficial relationship with *Perityle bisetosa*. The small habit, white-flowered discoid heads, and 2 main pappus bristles of *P. vitreomontana* are features which resemble those of *P. bisetosa*. However, leaf and flower morphology indicate a close affinity of *P. vitreomontana* with *P. rupestris* var. *albiflora*, and a close study of the pappus of *P. vitreomontana* shows a structure which is reduced and derived from the section *Pappothrix* type. Characteristically there are 2 or 3 prominent bristles of the pappus, but in each case vestigial nubs are present between the main ones. By examination of several individuals, and often in different florets of the same head, one may observe a larger number of prominent bristles, 4-10, and rarely even 10-20. Vestigial nubs are almost always present when less than 10-15 rather well-

formed bristles predominate. *Perityle vitreomontana* is regarded, therefore, as belonging with the section *Pappothrix*, a disposition also supported by general morphology and chromatographic data (Fig. 9; Powell & Tsang, 1966).

5. *Perityle cinerea* (A. Gray) Powell, sida 3: 278. 1968. Fig. 20.

Laphamia cinerea A. Gray in Torr., Bot. Mex. Bound. 82. 1859.

TYPE: TEXAS: on rocks near Escondido Creek, Sept., *Bigelow s. n.* (Holotype, GH! Isotypes, NY! US! Photograph, DS!).

Pappothrix cinerea (A. Gray) Rydb., N. Amer. Fl. 34: 27. 1914.

Plants 8-25 (45) cm high, tomentose-canescens, densely leafy; leaves opposite below, alternate above, 1.2-2.5 cm long, 0.9-1.8 cm wide, broadly ovate to subdeltoid, rarely subreniform, the margins deeply serrate with lobelets obtuse to acute, obtuse to acute at the apex, subtruncate to subacute at the base, tomentose-canescens, but veins still conspicuous; petioles 0.6-1.0 cm long; inflorescence of solitary heads or clusters of heads borne on rather stout peduncles, 0.3-1.0 cm long; heads narrowly campanulate, 0.8-1.0 cm long, 4-7 mm wide, sometimes partially obscured by subtending leaves; receptacle flattened, 1.5-2.0 mm wide; bracts 8-10, 5-7 mm long, 1.1-2.0 mm wide, keeled to obscurely so, tomentose, inner series essentially like the outer except more membranous along the margins and less pubescent; disc florets 10-15; disc corollas white, 5.3-6.0 mm long, the tube 1.3-1.6 mm long, minutely glandular-pubescent, the throat tubular, 2.8-3.2 mm long, sparsely glandular-pubescent, the lobes narrow, acute, reflexed, 0.8-1.2 mm long; achenes 2.6-3.0 (3.5) mm long, partially flattened; pappus of 14-20 slender bristles, the bristles unequal in length, but most are subequal, minutely antrorse-ciliate; anthers (2.3) 2.5-3.0 mm long; chromosome number, $n = ca. 68$.

Rare in crevices of Cretaceous limestone caprock of mesas. Spring-Fall (Fig. 17).

Representative Specimens:

TEXAS: PECOS Co: on rocks near Escondido Creek, Sept., *Bigelow s. n.* (GH, NY, US); 6 mi. e. of Bakersfield, April, *M. McKenzie 128* (SRSC); 7-Mile Mesa, near Ft. Stockton, 15 Sept. 1964, *A. M. Powell 1310* (SRSC); cracks in caprock, 17 July 1943, *B. C. Tharp 43-965* (TEX, US); limestone caprock and on top of mesa, 1 July 1943, *Tharp 43-966* (ND, POM, RM, SRSC, TEX, US); 7-Mile Mesa e. of Ft. Stockton, 16 Aug. 1962, *Warnock 20403* (SRSC); Ft. Stockton, 14 June 1907, *H. H. York 291* (DS, SRSC, TEX). UPTON Co: ca. 10 mi. s. of Rankin, Noltke Hill, 14 Sept. 1961, *Correll & Johnston 24607* (LL).

Plants of this species are strikingly cinereous. Individuals of a single population may be suffruticose and rather tall

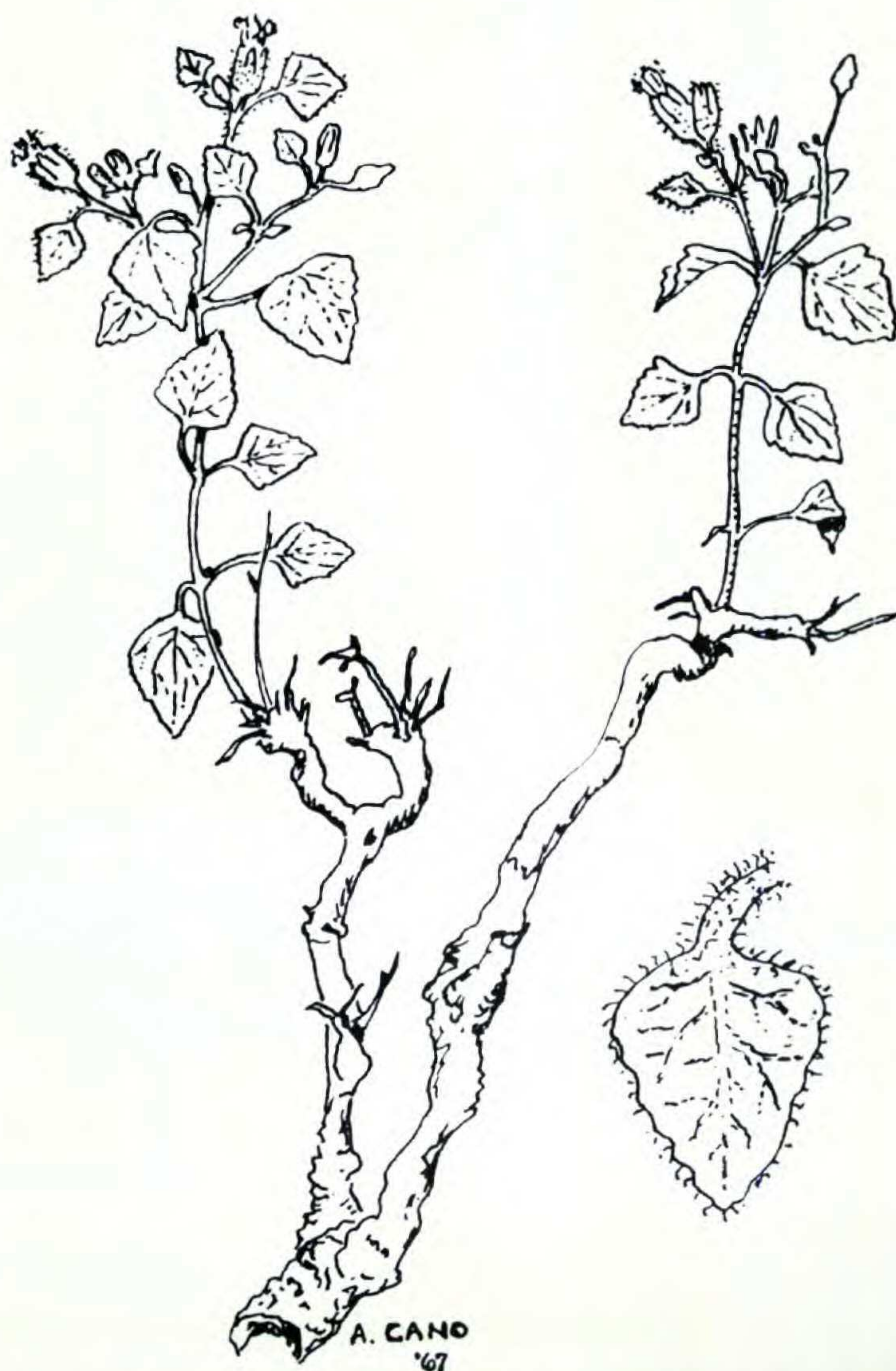


Figure 20. Habit sketch of *Perityle cinerea* (Powell 1310); $\times 1$.

or very short and appressed to rocks, at least in some instances depending on whether or not they are in reach of sheep which browse the plants. *Perityle cinerea* appears to be most closely related to *P. vitreomontana* or the white-flowered variety of *P. rupestris*, notwithstanding the tomentose-canescence pubescence which is not approached by any other species of the genus except the Guadalupe Island endemic, *P. incana*.

The type locality of Escondido Creek, now called Tunis Creek, is about 30 miles east of Fort Stockton. No plants of this species could be found in the small rock bluffs along

the creek, and this is not a typical habitat for *P. cinerea*. Therefore, it appears that the original collection was made somewhat near there but higher up on the mesas which abound in the area along the route taken by Bigelow's party.

The distribution of *Perityle cinerea* overlaps that of *P. angustifolia* (sect. *Laphamia*) along the Cretaceous cap-rock exposures in eastern Pecos Co. Plants of these two species have been observed growing side-by-side (but not extensively intermixed) about 6 miles east of Bakersfield. No interspecific hybridization has been detected, but fertile progeny would be unlikely since the chromosome number of *P. cinerea* is $n = \text{ca. } 68$ as compared to $n = 17$ for *P. angustifolia*.

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